

# *The importance of ecophysiology for both biotic and abiotic studies of the soil*

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## Summary :

The first part of this introductory paper addressed to the third plenary session is dealing with the definition of the word ecophysiology and its specific role in soil zoology. Contacts with a number of soil zoologists have been previously taken and a synthesis of their opinion is yielded in order to clarify our understanding of the significance of the term ecophysiology.

The second part shows through a number of recent examples the contribution made by ecophysiological works in the explanation of certain adaptive strategies adopted by animal species in order to survive and develop in the soil : mechanisms which account for the presence and development of soil fauna in cold regions; tolerance of low temperatures in soil microrthropods; classification of soil animal species according to their metabolism; influence of biological and environmental factors on the calculation of metabolic equations; water exchange between soil animals and the surrounding environment; analysis of transpiration rates according to the ecological localization of the species.

The third part considers the soil and its properties with respect to gases and water in the light of ecophysiological approaches. The notion of *capacitance* borrowed from physiologists permits to define organisms by the manner in which external systems respond to relative variations in the respiratory gases which are present; an acid soil behaves like a gaseous system while a calcareous clay soil is more like a water system. Biological consequences of this notion are examined. The desiccation of a slab of soil reveals a polyphasic phenomenon in which three categories of water succeed one another; the succession of these hydric states permits slow, gradual transition from an aquatic system towards a xeric aerial system. This desiccation process is characteristic of all hygroscopic materials and the soil is one member of the group of porous bodies (the term *porosphere* has been proposed as a collective category of all solids with an internal surface). Consequences of the thermodynamic properties of the soil for the evolution of soil fauna are discussed.

**Key words :** cold hardiness, metabolism, transpiration, soil capacitance, soil water, evolution of terrestrial faunas.

## I. Ecophysiology : definition and examination of its specific role in soil zoology

This is the first occasion on which ecophysiology has been represented as a principal theme in an International Colloquium on Soil Zoology. At previous conferences, few reports have been specifically devoted to ecophysiological studies of soil fauna. The fact that so few zoologists have been concerned with explaining the behaviour of soil-living animals in their natural surroundings is doubtless due to the relatively recent emergence of ecophysiology as a scientific discipline. Its foundations, essential concepts and methods are so far inadequately defined. The aim of this paper is to remedy this situation and, if possible, to contribute to the promotion of ecophysiology as one of the soil sciences.

Nowadays, ecophysiology has come to be recognised by a variety of branches of biology as a major scientific discipline which, as the name suggests, occupies the borderline between older-established disciplines : ecology and physiology.

Ecology was defined by HAECKEL in 1866 as a distinct biological science concerned with « the relation to its organic as well as its inorganic environment, particularly its friendly or hostile relations to those animals or plants with which it comes into contact »<sup>1</sup>. The term « ecology » is now widely known as referring to the science dealing with the conditions of life of living organisms and the combination of abiotic and biotic interactions connecting them with their environment. As a fundamental science « the task of ecology is the study of the functional organisation and evolution of biological systems corresponding to levels of integration equal or superior to that of the individual »<sup>2</sup>.

Physiology was defined in the 19<sup>th</sup> century as the science concerned with life processes and with the organic functions underlying them. The French physiologist Claude BERNARD added in 1867 that « Life can only be seen in terms of the conflict between the physico-chemical properties of the external environment and the vital properties of the organism, responding one to the other »<sup>3</sup>. In other words, the living

1 In GATES (1980), see references.

2 In « Logique et Unité de l'Écologie » (1981) rapport E.N.S. Paris n° 20.

3 Quotation in KAHANE (1962), « La vie n'existe pas », Éd. Rationalistes, Paris, 260 p.

organism is not « in itself » alive when separated from its environmental context; its fundamental characteristic was seen as the resultant of the interactions between the matter constituting the organism and extraneous matter. From this point of view, 19<sup>th</sup> century physiologists clearly adopted an ecological perspective in attempting to integrate life processes into a global system.

Today, the separation between ecology and physiology is becoming less and less distinct. On the one hand, ecologists require physiological explanations to advance their understanding of the causation of individual behaviour *in situ*, while on the other hand, physiologists are feeling the need to integrate the results of their research within a framework which takes into account the constraints exerted by the external environment. « Physiology is about the functions of living organisms — how they eat, breathe and move about, and what they do just to keep alive... Physiology is also about how the living organism adjusts to the adversities of the environment... Finally, physiology is about the regulation of all these functions — how they are correlated and integrated into a smoothfunctioning organism » (SCHMIDT-NIELSEN, 1979).

It is nevertheless possible to identify areas of research which are proper to either ecology or physiology. Whereas research into autoecology is connected with physiology, study of populations and biocenoses represents a domain which is restricted to ecology, with its own methods and concepts that have revealed novel properties in the organisation of biological systems. Similarly, physiology covers a field of investigation which cannot be claimed by any other branch of biology, namely the study of functions and properties of organs and tissues of living organisms. It is well known that this area of research has been extremely productive in its own right, yielding numerous practical applications, notably in medicine.

The role of ecophysiology is precisely that of operation between the two fundamental areas belonging to ecology and physiology, and of establishing bridges between the two disciplines. Physiologists and ecologists have agreed in defining the concepts and methods utilised in ecophysiology. The result of their deliberations is embodied in the general definition published in 1980 by the Société française d'Eco-physiologie, which I quote in full :

« Ecophysiology, the science concerned with interactions between organisms and their environments, involves both the descriptive study of the responses of organisms (isolated or in groups) to ambient conditions and the causal analysis of the corresponding ecologically dependent physiological mechanisms, at every level of organisation.

These physiological mechanisms are examined not so much in their own right as with respect to their adaptive significance. For this reason, the ecophysiological approach must take into account polymorphism in individual responses, which are largely responsible for the adaptive capacity of any given population. In this respect, ecophysiological study yields information which is fundamental for an understanding of the mechanisms underlying adaptive strategies.

Ecophysiological research is conducted not only on organisms in their natural environments but also under conditions disrupted, manipulated or even created by human intervention.

One of the prerequisites of ecophysiological research is, accordingly, the acquisition of detailed knowledge of the environments concerned, along with experimental control of their specific parameters. A given environment results from a highly variable combination of factors, be they physical (incident radiation; temperature; humidity; pressure, etc...), chemical (nutritive or non-nutritive) or biotic (ecomones; pheromones; social factors; parasitism; etc...). In addition, all environments are subject to varying degrees to factors exhibiting periodic variation, which can again be physical (photoperiod; thermoperiod; etc...), nutritional or biotic. The influence of such factors as synchronizers of physiological rhythms (e.g. circadian; lunar; circennial) must be studied as well.

From a methodological point of view, the ecophysiological approach can and should be concerned not only with global physiological responses to variations in a complex environment, which are best studied under natural conditions, but also with the isolated effects of each of the factors involved and with their interactions. In this latter context, laboratory experimentation and studies conducted in experimental environments are undoubtedly most appropriate. Hence, ecophysiological studies require a systematic effort to match laboratory experiments with observations conducted in the natural environment.

Defined in this way, ecophysiology provides a source of explanatory principles for ecological data and contributes to the identification of the ecosystems in which all living organisms are integrated.

As man's possessive and technological grasp is progressively expanded around the world, the real environment in which plants, animals and man himself exist is becoming radically altered from its original state and with increasing rapidity. Environments and ecosystems are being subjected to transformation and pollution which can involve the qualitative addition of factors normally absent or the quantitative modification of existing factors. All of this results in the disruption of biocenoses and their inherent biotic factors.

The ecological approach to these modifications and disruptions is essentially descriptive; only an ecophysiological approach can provide an explanatory basis. Ecophysiology yields the scientific foundation for the controlled modification of natural environments and for the definition of optimal, acceptable norms for the creation of artificial environments (habitats with a large technological component; sites for work or habitation isolated from the natural environment — whether terrestrial, subterranean, submarine, aerial or extraterrestrial, in which both man and animals are found with increasing frequency and for increasingly long periods). Changes in environment are also becoming more and more frequent and abrupt, especially in the modern world. Such changes give rise to physiological disorders and desynchronization of biological rhythms, effects which can be understood through ecophysiological studies and which have important socio-economic and medical consequences.

With animals and plants, ecophysiological studies contribute to the optimisation of techniques of husbandry and agriculture, with the aim of improving foodstuffs and industrial products.

In this vast research field devoted to the influence exerted by the environment on the physiological functions and performance of living organisms, the dissemination of fundamental knowledge can take place very rapidly and it is easy to achieve a close linking of fundamental and applied research.

Thus, whether carried out « in the field », in reconstituted biotopes or in bioclimatic laboratories, whether involving wildliving species, domesticated or cultivated species of economic importance, or man himself, the most « fundamental » ecophysiological research eventually contributes to areas which occupy a prime place in human preoccupation and responsibility: the conservation of natural faunas and floras and — for man himself — the improvement of animal and plant food products, the protection of an optimal « quality of life » and the assurance of good health, or perhaps even human survival ».



I have myself contacted a number of soil zoologists in order to clarify my understanding of the significance of the term « ecophysiology ». In fact, some of them pointed out that it is difficult to define the exact contours of ecophysiology and that the best means of identifying this new discipline in soil zoology remains that of demonstrating reliable and convincing results which are statistically significant and can be applied by ecologists in the context of animal populations living in their natural biotopes. Others felt that there was no need to explain the behaviour of soil animals, arguing that the aim of studies in soil zoology is primarily that of finding a solution to the problems of management of soil environments and that for this it is not necessary to understand the functioning of soil organisms down to the molecular level. It must also be recognised that the education given to ecologists does not prepare them for involvement in programmes of ecophysiological research and that it is preferable for them to participate in programmes in collaboration with colleagues possessing a formal background in physiology.

In order to gain admittance to the domain of soil zoology without reservation, ecophysiology must first of all demonstrate its validity and utility. Those who have chosen to present their work at this third session of the Eighth International Colloquium of Soil Zoology will attempt to pass this examination with flying colours.

The responses from my informants also included a number of positive replies and these exhibited a common denominator which, to my mind, marks out ecophysiological studies from both ecological and physiological research : this resides in the notion of function and the adaptation of species to their natural environments. I shall summarise in a few lines the observations and propositions which have been made to emphasize the importance of ecophysiology for soil zoology :

1. Ecophysiology is really the functioning of the animal/plant in its normal environment, so studies in this discipline should be based on field data and conditions. Ecophysiology has the challenging opportunity of attempting to bridge the great gap between what the animal does in nature and its performance in laboratory situations. This is one of the most important areas in ecology-physiology, because one without the other is virtually useless.

2. If in soil biology we are to try and gain an understanding of the natural processes that occur within terrestrial systems, then studies of both structure and function are necessary. These can be undertaken at all levels of organisation and most ecophysiologicalists have concentrated on the individual animal, species or population. Often in ecology an explanation without reference to the physiology of the animal concerned is incomplete. But that is not to state that a study of the physiology of a species will answer all questions.

3. In many ways, physiological work in relation to relevant environmental factors will tell us why an animal is found, where it is and how it lives there. The ways in

which species are adapted, physiologically, to withstand changes and fluctuations in physical conditions surely constitute the field of the ecophysiologicalist, in that here he is at the very interface of the species with its physical and biological environment.

4. In order to ensure the maintenance of their principal vital functions (respiration, digestion, excretion, reproduction), all living organisms exchange matter and energy with their surroundings. These exchanges depend upon the laws of diffusion established by physicists and chemists and cannot be ignored by ecophysiologicalists concerned with the evaluation of energy costs or transfer of matter at the level of the individual organism. Such studies are distinct from those conducted in the field of bioenergetics. In fact, « bioenergetics is the term used to denote the study of energy transformations in living organisms. Since the cell is the basic unit of structure and function in living organisms, biological energy transformations are most fruitfully considered at the cellular level. The bioenergetics of the cell is a central element in the study of biochemistry and biophysics, and thus, of the field of molecular biology » (LEHNINGER, 1965).

While the ecophysiologicalist can contribute much to soil zoology, the latter can in turn promote the development of this new discipline by presenting it with original and fundamental topics for research. Soil zoology is, in fact, notable for its interest in animal species which are for a large part primitive forms, morphologically close to those which participated in the great transition from the aquatic environment to a free-living terrestrial sphere in the Palaeozoic era. Even today, soil animals exhibit the entire range of adaptive mechanisms for life in air, from the simplest (cutaneous respiration) to the most complex (tracheal systems; lungs). Thus, comparative ecophysiology of soil animals has a great future in the realm of evolutionary biology.

It must also be emphasized that ecophysiology, just like physiology, is built upon the experimental method and is logically dependent upon reductionist approaches. These involve the isolation of individual factors, major biotic or abiotic components of the environment, to determine their influence upon individual behaviour. In some cases, it is necessary to test the potential of individual animals to tolerate a given climatic component (temperature; humidity; partial pressure) beyond the normal limits recorded under natural conditions. The resistance of a species to abrupt fluctuations of a particular environmental parameter not only reveals its enhanced capacity to colonise new habitats or to survive an ecological catastrophe, but may also bear witness to an ancient adaptation which is still incorporated in the genetic code. For example, some species which are now confined to subterranean environments characterised by constant high humidity still exhibit a great capacity to withstand desiccation.

My essential mission is that of promoting ecophysiology to my ecological colleagues, for physiologists have for some time been convinced of the need to integrate their results in the broad context of the environment. Some physiologists willingly

leave their laboratories to take part in ecological research programmes, whereas too few ecologists are prepared to reciprocate. Yet this is precisely the more that must be made. My personal conviction is that ecophysiological studies are best developed by biologists with long-standing practical experience of field work. The best arguments for introducing ecophysiology into the domain of soil zoology are to be found in recent syntheses published by authors with an initial training in ecology : CRAWFORD (1981), EDNEY (1977), GATES (1980), SCHMIDT-NIELSEN (1979), THIELE (1977).

## II. The contribution of ecophysiology to research on soil animals

It is not my intention to attempt a synthesis of all of the problems resolved by ecophysiological studies in soil zoology. Instead, I wish to show through a number of recent examples the contribution made by ecophysiological research in the explanation of certain adaptive strategies adopted by animal species in order to survive and develop in the soil.

### 1. Tolerance of low temperatures in soil microarthropods

In polar or alpine regions soil animals are subject to intense cold, which slows their metabolism and hence leads to considerable restriction of motor activity, digestion and growth. The role of ecophysiology is that of identifying the adaptive mechanisms which account for the presence and development of the soil fauna in polar regions.

The first problem which must be resolved is that of explaining how the animals concerned are able to resist freezing conditions. The goal of research in this area (see the synthetic article written by BLOCK, 1980) is that of defining the physiological/biochemical mechanisms which allow poikilothermous invertebrates to tolerate cold by using one of two strategies, freezing susceptible or freezing tolerant. In the former, the animal is killed by the freezing process and its defence is to avoid this by supercooling (maintenance of the body fluids in a liquid state below the normal freezing point), which may be enhanced by the presence of polyhydric alcohols and sugars in the body. In the latter, the animal survives extra-cellular freezing which occurs at relatively high sub-zero temperature due to ice nucleators which are present in the body. Glycerol may play an important role in the protection of freezing tolerant species by reducing cell damage.

The main techniques employed in these investigations are determination of individual supercooling points (point of origin of a small, but significant, rise in body temperature that accompanies emission of latent heat during freezing), measurement of

freezing points of samples of body fluids, determination of lower lethal temperatures, study of chill coma behaviour, and the quantitative analysis of body fluids for cryoprotectants by paper, thin layer and gas-liquid chromatographic techniques.

Two microarthropod species living on Signy Island close to the British Antarctic Survey research station (60° 43'S, 45° 36'W) provide examples illustrating the adaptation of the soil animals to polar life conditions (BLOCK *et al.*, 1978). The two species are : *Alaskozetes antarcticus* (Michael), Acari, *Cryptopygus antarcticus* Willem, Insecta, Collembola. In the Antarctic region, the minimum air temperature in winter can fluctuate between - 25 and - 40° C, and these animals can be subject to temperatures of - 20 to - 25° C in the soil.

Both species concerned exhibit a supercooling point between -25 and -30° C, such that they can survive without difficulty in their biotope. Other ecophysiological measurements have shown that the supercooling level depends heavily on nutritional activity. Fasting animals exhibit a significantly lower supercooling point than those which have been feeding. This result suggests that the presence of food in the digestive tube increases the probability of freezing occurring in a supercooled animal because such material contains efficient nucleating agents. Glycerol is the main polyol concerned in the mites, for which a direct relationship exists between its concentration in the body fluids and the level of supercooling, whereas sugars appear to be more important in collembolans. Low temperature and desiccation (40-50 % R.H.) bring about significant increases of cold tolerance in all species examined. The nymphal stages of the cryptostigmatid mite are, in fact, more hardy than the adults.

All microarthropods studied have proved to be freezing susceptible and only a single Antarctic species of midge larva, *Belgica antarctica*, has been found which tolerates freezing. It is likely, however, that additional freezing tolerant forms may be present among the higher insects and arachnids in polar regions.

The results of ecological research are not limited simply to the discovery of the adaptive mechanisms of individual species. It is also possible to ask more far-reaching questions, for example about the evolutionary history of the fauna. The present pattern of distribution of animals in the polar regions poses a fundamental question : has the colonization of cold environments by such animals necessitated the evolution of specific and novel physiological and/or biochemical mechanisms, or are the mechanisms utilised the result of development and extension from some pre-existing basis ? (BLOCK, *in litteris*). Some work has been undertaken, mainly in Arctic environments, which suggests that freezing tolerant species are relatively uncommon and that this strategy has been adopted by larger and more highly organized arthropod forms that overwinter.

A second fundamental aspect of the survival strategy of soil animals adapted for cold conditions has been demonstrated by BLOCK & YOUNG (1978) using respi-



ratory microtechniques (Cartesian diver microrespirometer) which permitted them to measure the standard metabolism of the oribatid mite *Alaskozetes antarcticus* as a function of temperature. As a general rule, the presence and maintenance of a species in a given biotope implies positive production on the basis of the energy assimilated in order to permit the generation of its own tissues and reproductive output. The basic energy equation, of course, reads as follows :

$$\text{Assimilation} = \text{Respiration} + \text{Production}$$

According to MACLEAN (1975), there are three different patterns which can be recognised : in type I, assimilation rate is greater than respiration rate at all temperatures encountered by the animal, thus allowing a favourable energy balance (production is positive). In type II, assimilation rate increases more rapidly with rising temperature than respiration rate and thus the amount of energy available for growth increases with temperature. Such an animal may be unable to complete its life cycle at low temperatures because of an unfavourable energy balance (production is negative at low temperatures). Type III, respiration rate increases more rapidly with temperature than assimilation rate. This is the pattern of an obligate polar species, which is able to maintain a positive energy balance only at low temperatures (production is only positive at low temperatures). Polar terrestrial invertebrates may be grouped under type I or III.

BLOCK & YOUNG (1978) in fact demonstrated that the standard metabolism of the mite *Alaskozetes antarcticus* was, at 0°-5° C, close to that of temperate region species at 10°-15° C. This indicates that the elevation of metabolic rate at low temperatures represents an adaptation in poikilothermous animals living in polar regions.

## 2. An attempt to classify animal species according to their metabolic turnover

Ecophysiologicalists have for some time been seeking to characterise soil-living animal species on the basis of the allometric relationship between the consumption of oxygen and live or dry body weight. Techniques of respirometry are continually refined through miniaturisation and improvements in sensitivity. The microrespirometer with variable pressure and volume described by VERDIER in this session is the most recent example of the introduction of a new principle of measurement.

Ecologists are interested in respirometric techniques as a means of characterising different trophic levels in the soil. In this context, respiration represents a comparative parameter expressing the quantity of energy dissipated by a given population.

Quite apart from demonstrating that respirometric techniques provide an excellent tool for revealing the degree of adaptation of individual species to their environments with respect to the availability of food resources in the soil, the ecophysiologicalist must also conduct a critical examination of the principal parameters which may influence the calculation of metabolic equations :

a. Respirometric techniques must take account of the structure of animal populations. For example, with the oribatid mite *Alaskozetes antarcticus* the metabolic rates measured at 10° C vary considerably according to the stage of development :  $510.66 \pm 55.90 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for the larva;  $359.37 \pm 25.24 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for the protonymph;  $257.30 \pm 14.56 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for the deutonymph;  $208.00 \pm 21.01 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for the tritonymph; and  $170.96 \pm 8.41 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for the adult (YOUNG, 1979). In ametabolous insects such as collembolans which exhibit continuous growth through a series of moults before reaching maximum size, individuals of a given species can be grouped into size classes (TILBROOK & BLOCK, 1972) before measuring the metabolic rates of each class. In *Cryptopygus antarcticus* conditioned to a temperature of 10° C, BLOCK (1978) determined the following values :  $539.68 \pm 77.16 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for class I (440-750  $\mu\text{m}$ );  $326.76 \pm 40.10 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for class II (750 - 1 060  $\mu\text{m}$ );  $308.53 \pm 77.54 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for class III (1 060 - 1 370  $\mu\text{m}$ );  $221.90 \pm 9.87 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for class IV (1 370 - 1 680  $\mu\text{m}$ ).

These results clearly demonstrate the difficulty involved in characterising a species by a single value for its metabolic rate without taking into account the principal post-embryonic stages of development. They reveal to the ecologists the fact that the role played by saprophagous insects in the degradation of organic matter is greater for immature stages than for adults.

It is sometimes possible to find a significant difference between the two sexes in their metabolic rates, despite the absence of any difference on size between males and females. Among Collembola, *Orchesella cincta* exhibits a metabolic rate at 15° C of  $417.01 \pm 6.3 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for males and a rate of  $391.2 \pm 2.4 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for females, while in *Tomocerus minor* the rates are  $345.6 \pm 9.3 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  for males and  $356.4 \pm 5.4 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  (TESTERINK, 1981).

b. Temperature has a marked influence on measures of metabolic rate in soil animals, and the degree of influence varies according to the stage of development. For example, in the mite *Alaskozetes antarcticus* the larva consumes  $160.98 \pm 37.81 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  at 0° C,  $288.22 \pm 22.22 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  at 5° C and  $510.66 \pm 55.90 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  at 10° C, whereas the tritonymph consumes only  $133.83 \pm 4.96 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  at 0° C,  $200.25 \pm 12.79 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  at 5° C and  $208.00 \pm 21.01 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  at 10° C (YOUNG, 1979). In ametabolous insects, the same phenomenon is observed in comparison among size classes.

c. The relative humidity of the air (R.H.) or the saturation deficit (s.d.) can also influence the metabolism of soil animals. In my own laboratory, we have demonstrated the decisive influence exerted by air humidity on measures of metabolic rate obtained for the collembolan *Willowsia buski* at 20° C :  $0.848 \pm 0.95 \mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$  at 98 % R.H. (s.d. = 1.034 mm Hg);  $0.987 \pm 0.093 \mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$  at 95 % R.H. (s.d. = 1.068 mm Hg);  $1.277 \pm 0.177 \mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$  at 75.5 % R.H. (s.d. = 1.200 mm Hg); and  $1.418 \pm 0.287 \mu\text{l O}_2 \text{ mg}^{-1} \text{ h}^{-1}$  at 65 % R.H. (s.d. = 1.267 mm Hg) (unpublished results obtained in collaboration with VERDIER).

d. Measures of metabolic rate change as a function of the time for which the animals concerned have been maintained in captivity. Captive collembolans can exhibit considerable reduction in metabolic activity. Individuals of the species *Cryptopygus antarcticus* in the size-class 1 060 - 1 370  $\mu\text{m}$  maintained in captivity at 5° C have a mean metabolic rate of  $259.90 \pm 96.86 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  on the first day following capture. After 4 days in captivity their mean metabolic rate is  $215.11 \pm 11.09 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$ , falling to  $136.49 \pm 43.82 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  after 86 days and after approximatively one year in captivity the rate is no more than  $81.04 \pm 15.86 \mu\text{l O}_2 \text{ g}^{-1} \text{ h}^{-1}$  (BLOCK, 1977). This decline in metabolic activity is doubtless a general phenomenon among such animals in captivity and may be explained either by alteration in feeding conditions or on the basis of individual capacity to tolerate partial fasting. After a few days fasting, the allometric equation relating respiration (R) to live body weight (W) is modified in the collembolan *Tomocerus minor*, from  $R = 0.269 W^{1.067}$  for individuals fed at 10°C to  $R = 0.200 W^{0.804}$  after 3 days of fasting (VANNIER, unpublished data).

In the light of these comments, it is easier to understand why ecophysiologists carry out their measurements as close as possible to the natural areas of occurrence of soil animals, in order to reduce the time elapsing between capture and experimental manipulation. Even when a wealth of precautions is taken to reconstitute natural environmental conditions within laboratory measuring chambers, it must be admitted that it is not a simple matter to characterise the metabolic activity of a given species with a single allometric equation. Clearly, numerical values for metabolism must be handled carefully prior to incorporating them in global energy balance calculations.

Nevertheless, we must not allow these difficulties to prevent us from establishing relationships between metabolism and the position occupied by individual species within the soil system. PETERSEN (1980, 1981) undertook the study of the respiratory metabolism of 11 collembolan species living in a mull soil in a Danish beech forest. His results from respirometry experiments carried out with an open gradient diver method suggest that the rate of oxygen uptake decreases from epiedaphic through hemiedaphic to euedaphic species. This relates to a general law of soil ecology according to which the metabolic level of animals decreases as a function of the depth at which they live. Comparative study of respiration in two collembolan species, one living at the soil surface (*Tomocerus minor*) and the other living in caves at depths of up to 100 m (*Tomocerus problematicus*), provides a good illustration of this principle (VANNIER & VERDIER, 1981). At 10° C,  $R = 0.913 W^{0.73}$  ( $r = 0.91$ ) for *Tomocerus minor*, whereas for *Tomocerus problematicus*  $R = 0.74 W^{0.86}$  ( $r = 0.96$ ).

### 3. Water exchange between soil animals and the surrounding environment

The responses of animals to variations in the water relations of the soil constitute a research topic involving both ecological and ecophysiological approaches in soil zoology.

Ecological studies are concerned with the elucidation of the behaviour of soil animal populations during the seasonal cycle and with the identification of species which are either sensitive to or indifferent to drought or excess water in the soil. Research in this area has led to formulation of the general concept of water accessibility for animals, just as botanists at the turn of the century had been led to the concept of water availability for plants : « Soil animals are only affected by progressive desiccation of their substrate beyond a critical level of humidity which is constant for each group of species. This critical level is an indicator of the retention forces which dry matter exerts on water and which animals are unable to oppose. As long as the critical threshold of humidity is not attained, individuals of any given species are able to use water to maintain their water balance ». (VANNIER, 1970, 1971).

The limit of water availability for certain isotomid Collembola is found at pF 4.2, that is to say where water is retained by soil particles with a force of  $15.8 \text{ kg cm}^{-2}$ , while in certain oribatid mites it is found in the region of pF 5, corresponding to a binding force between water and the soil of  $100 \text{ kg cm}^{-2}$  (VANNIER, 1970).

Study of water balance, defined as the state of equilibrium between gain and loss body water accompanied by all of the adaptive mechanisms involved in the maintenance of this balance, is an ecophysiological research topic which permits evaluation of the degree of adaptation of individual species to their surroundings or to climate in general. In establishing the water balance of a species, the ecophysiologicalist should evaluate losses of water through transpiration, respiration and excretion, together with gains through intake of solid or liquid food, through the oxidation of tissue reserves (1mg of fat can yield 1.07 mg of water), and through active or passive absorption of atmospheric water.

Water exchanges between an animal and the external environment represent a subject which is by far one of the most intensively studied in soil zoology. A soil invertebrate which is unable to re-establish its water balance by absorption of water in the liquid state has two means of effectively resisting evaporation. The first permits the animal to maintain its weight constant thanks to the intake of atmospheric water above a critical relative humidity value for the surrounding air. This capacity to extract water vapour from the surrounding air is highly developed in arthropods occupying specialized ecological niches, such as the dust mites and ectoparasites. Extraction of water vapour is less specialized than the phenomenon of anhydrobiosis; it is found in a wide range of zoological groups including Thysanura, cockroaches, Orthoptera, Psocoptera, Siphonoptera, Mallophaga and keratophagous moths (EDNEY, 1977). The second means of resistance resides in the limitation of the transpiration rate at a minimal, constant level independently of the time elapsed and body water content (autoregulation or homeostasis).

Gravimetric methods are generally predominant in the measure of water transfer. However, they are not suitable in all cases since they only assess the net flux of sorp-



tion or transpiration. When an animal is in balance with the ambient vapour pressure, the number of water molecules escaping from its body is equal (over a given period of time) to the number of water molecules entering its body (Transpiration = Sorption). These continuous exchanges cannot be detected by a microelectrobalance as no variation in mass can be recorded. In such cases, tritiated water (HTO) is employed as a tracer. In order to study sorption, the animals are placed in an atmosphere containing tritiated water vapour and their level of radioactivity is then measured at regular intervals. Study of transpiration is carried out in the same way by first placing the animals in an atmosphere containing tritiated water vapour until equilibrium has been reached and then moving them on to a chamber without tritiated water in order to measure the decrease in their tritium content. This technique of using a radioactive tracer was described by WHARTON & DEVINE (1968), whose research was concerned with mites. Recently, in a review paper covering insects and mites, ARLIAN & VESELICA (1979) have set out the fundamental principles of the radioactive method.

Most animal species living in the soil are unable to extract water vapour from the atmosphere even when the air humidity level is close to saturation. For such species, the microgravimetric method is the most convenient for measuring losses of body water through transpiration. When the aim is to demonstrate the potential capacity of a species to resist desiccation, it is possible to study the progress of its transpiration rate in a totally dry atmosphere (R.H. = 0 %) in order to measure absolute flux values. The results of such research are presented in the form of a diagram borrowed from physicists specifically concerned with questions of desiccation (KNEULE, 1964). The ordinate represents the transpiration rate in grammes or milligrammes per unit time (hour or minute), while the abscissa represents water content as a percentage of dry weight. In this way, one can obtain a more informative representation of the process of transpiration than with a simple curve showing change in body weight or percentage thereof as a function of time. The elimination of the temporal factor and its replacement by body water content permits direct comparison between species or individuals of different size.

Among collembolan insects the mode of transpiration differs according to the ecological localization of the species, ranging from epigeous to endogeous zones. Analysis of transpiration diagrams from a wide variety of species has permitted me to recognize three types of adaptation to an edaphic existence :

a. Type I (hygrophilic) includes all forms which exert no control at all over their loss of body water, such that water transfer takes place as a simple diffusion phenomenon (perspiration). The profile of the curve resembles that obtained for drying of inert hygroscopic matter, e.g. *Tetrodontophora bielanensis* from the wet forest of Central Europe.

b. Type II (mesophilic) includes species which exhibit a transpiration curve profile with a plateau indicating that the rate of body transpiration is maintained constant

independently of the reduction of internal water content (regulatory phenomenon), e.g. *Tomocerus minor*, species living below the litter layer of temperate forests.

c. Type III (xerophilic) also exhibits the phenomenon of regulation of transpiration rate, but with the capacity to maintain it at a level considerably lower than that found with type II. The plateau region of the curve is terminated by an abrupt increase in transpiration rate, followed by a rapid decrease leading to total desiccation of the animal. Resistance to desiccation in the animals concerned is so pronounced that it is necessary to calculate transpiration rates in terms of hours, whereas with type I and II a measurement in terms of minutes is sufficient. Examples are provided by *Seira domestica* which lives in domestic dust and by *Allacma fusca* the adult stage of which lives in the herbaceous level of temperate forests.

Data on these aspects are combined with other information on resistance to diffusion of water vapour, the effects of moulting on water balance and the role played by the internal environment in transpiration, in an ecophysiological synthesis concerned with the resistance of the first terrestrial arthropods to desiccation (VANNIER, 1978).

Great differences can exist between sympatric or coexisting species with respect to both the rate of water uptake and the rate of water loss. VERHOEF (1978) has compared two springtail species living in the same Dutch forest litter. *Orchesella cincta* has, on average, a lower transpiration rate and a higher rate of water uptake than *Tomocerus minor*. As the critical level of water content is approximatively the same for both species, *Tomocerus minor* is much more drought-sensitive than *Orchesella cincta*. The former species can be regarded as being drought-sensitive throughout its entire life-cycle, whereas the latter is drought-sensitive only during its egg stage and during its moulting stage. Consequently, during dry summers *Tomocerus minor* is found mainly in wetter areas, whereas *Orchesella cincta* is also found in dry areas.

Transpiration curves do not only reveal differences between species. Like allometric curves for metabolic rate, they also characterise different developmental stages of a single species. In collembolan *Allacma fusca*, xerophilic capacity is acquired in the course of ontogeny. In fact, the hatching stage is unable to regulate its transpiration rate and behaves like animals of the meso-hygrophilic type. This sensitivity to the evaporative power of the air constrains individuals which have just hatched to maintain contact with the soil in humid areas and obliges the species as a whole to remain beneath forest cover. Yet the great degree of resistance of adults to desiccation would permit migration to open environments such as grasslands (BETSCH & VANNIER, 1977).

At this point of my survey, I would like to emphasize the value of ecophysiological tests carried out under experimental conditions which elicit from animals responses they no longer exhibit in the natural biotope. When experimentation is conducted under conditions close to those prevailing in the natural surroundings, it is not always

possible to identify differences in metabolism and heat-sensitivity between species belonging to the same phylogenetic group. It must be accepted as a general rule that when the speciation process is initiated, physiological functions are the first to be affected before far-reaching morphological or anatomical changes take place.

Experiments involving the subjection of an animal species to progressive increase in temperature passing even beyond the lethal threshold, whilst controlling transpiration rates, allow us to separate two species which are impossible to distinguish under the optimal thermal conditions present in the natural biotope. Such experiments conducted on two collembolan species, the litter-living *Tomocerus minor* and the cave-living *Tomocerus problematicus*, show that it is impossible to find any statistically significant difference between their rates of transpiration at temperatures between 10° C and 15° C. However, at temperatures above 17° C, the transpiration rates calculated as a function of temperature increasing to 40° C are clearly distinct in terms of both average values and their standard deviations (VANNIER & VERDIER, 1981). The same method applied to a wingless dipteran species, *Anatalanta aptera*, found on subantarctic islands revealed that the imago has lost the capacity of resistance to desiccation and high temperature which is well developed in winged dipterans. The adults of *Anatalanta aptera* have become mesophilic like most arthropods which live in permanent contact with humid soil (VANNIER, 1981).

There are many gaps in our knowledge of the physiological adaptation of soil animals. Although limitation of water loss resulting from transpiration is one of the most important traits of soil animals well adapted for living in the atmosphere, very little indeed is known about other aspects of their physiology, behaviour or population dynamics. Ecophysiologicalists still have a lot to learn from field studies. For example, the behaviour of certain cryptozoic species which emerge from the soil during the night or early morning is still poorly understood. EDNEY (1968) mentions the case of isopod crustaceans and suggests that terrestrial animals may sometimes be subject to an excess of water, requiring behavioural mechanisms that permit elimination of water as well as its retention, according to the needs of the moment.

### III. The contribution of ecophysiological methods to our understanding of soil biology

Measurements of metabolism or of water transfer are not only applicable to the living world; they are commonly utilised by ecologists to establish energy and water relationships for the soil in general. It is not my aim to point out the goals and value of such studies, but rather to take a fresh look at its specific properties with respect to gases and water in the light of ecophysiological approaches.

## 1. Study of the behaviour of O<sub>2</sub> - CO<sub>2</sub> in the soil : the notion of capacitance

The soil is a living thing whose metabolism can be studied from a physiological standpoint. Of course, it is the various organisms (microbes, plants and animals) living within the soil which are responsible for this metabolic activity. In the modern field of respiratory physiology a living organism is considered as « a system of gas exchange » (DEJOURS, 1975) characterised by the dynamic exchanges between the internal and the external environments. The properties of the internal and external environments in relation to the respiratory gases reflect these exchanges and the response capacity of any given animal species.

An animal takes up oxygen from its surroundings and expels carbon dioxide. Concentrations and partial pressures of O<sub>2</sub> and CO<sub>2</sub> in ambient media show patterns of change which are fundamentally different in water and air systems. Physiologists employ the capacitance coefficient to characterise the internal and external environments of an animal.

The capacitance coefficient ( $\beta_x$ ) of a medium for a given type of gas is defined as the increment of concentration ( $C_x$ ) for an increment of partial pressure ( $P_x$ ) :

$$\beta_x = \Delta C_x / \Delta P_x$$

In dimensional terms, this amounts to (quantity of substance). (volume)<sup>-1</sup>. (pressure)<sup>-1</sup>, which is identical in form to the solubility coefficient. The capacitance coefficient is a general term including not only physical solubility and chemical binding of a gas in a liquid, but also a property formally designating « solubility » of a gas species in a gaseous medium (PIIPER *et al.*, 1971).

The notion of capacitance hence permits us to define the aquatic or aerial nature of the respiration of a living organisms by the manner in which systems respond to relative variations in the respiratory gases which are present (Fig. 1).

When one adds a given amount of CO<sub>2</sub>, or subtracts the same amount of O<sub>2</sub>, to or from a gas phase, the change of partial pressure is the same for both gases ( $\beta_{CO_2} = \beta_{O_2} = 1/RT$ , where R is the gas constant and T the absolute temperature). In air, the capacitance coefficients of CO<sub>2</sub> and O<sub>2</sub> are identical (Table I). In water, on the other-hand, the change of partial pressure is 29 times greater for O<sub>2</sub> than for CO<sub>2</sub>, the difference being due to the low solubility of oxygen in water. Table I shows that the solubility of CO<sub>2</sub> is approximately the same in air as in water. The complexity of biological internal environments has entailed a pronounced increase in the capacitance coefficient for O<sub>2</sub> and CO<sub>2</sub>, as in human blood and in the haemolymph of sea-living crustaceans (Table I).

According to DEJOURS (1975), it may be said that in air-breathing animals changes of P<sub>O<sub>2</sub></sub> and P<sub>CO<sub>2</sub></sub> in the breathing process are approximately the same. In



Changes in partial pressure of  $O_2$  and  $CO_2$  in air and water (Fig. 1) have important biological consequences :

a. In an aquatic environment, a large volume of water must come into contact with the respiratory surfaces in order to ensure a supply of oxygen for an organism. An aquatic animal cannot endure for any length of time a  $P_{CO_2}$  of 5 mm Hg at  $10^\circ C$  without being forced to seek out air to obtain the oxygen it requires. This value represents the theoretical limit imposed upon aquatic animals (HOWELL *et al.*, 1973).

b. In an aerial environment, on the other hand, respiratory exchanges need only relatively small volumes to ensure the renewal of oxygen supplies for an organism.

All of these background elements are involved in the definition of different types of respiration which have been developed in soils. As I emphasize in this last part of my review, the soil must be considered as a specific environment comparable to water and air. It was from this standpoint that VERDIER (1975) studied the behaviour of oxygen and carbon dioxide in two types of soil :

a. An acid soil (podzol) with its humidity level adjusted to field capacity (pF3) and subject to prolonged confinement behaves like an air-breathing system.  $P_{O_2}$  and  $P_{CO_2}$  show parallel changes in the atmosphere of this soil (Fig. 1).

b. A calcareous clay soil (rendzine) behaves like a water-breathing system under the same conditions of confinement. In the atmosphere of this soil,  $P_{CO_2}$  increases only very slowly while  $P_{O_2}$  falls abruptly (Fig. 1).

The capacitance for  $CO_2$  of calcareous clay soil has been calculated as pF3. Within the limits of the  $CO_2$  pressures observed *in situ* (from 0.2 to 4 mm Hg), the capacitance coefficient was found to vary from 5 300 to 2 600  $\mu M$  per litre of soil solution and per millimetre of mercury. These values are considerably higher than those presented in Table I and they may accordingly be of great biological significance.

## 2. Biological consequences of the capacitance of soils

The transition from aquatic to terrestrial life has led to slow, progressive development of respiratory mechanisms in animal species. These processes are closely associated with the progressive increase in oxygen pressure in the atmosphere and the rise in temperature. The great majority of soil animals are extremely sensitive to a saturation deficit in the air and in most cases the exchange of respiratory gases takes place through the integument, which is a reflection of their aquatic origin.

Animal species which emerge from the soil and which live in a nonsaturated atmosphere must ensure the conservation of their body water by increasing their cuticular resistance to the diffusion of water vapour. This adaptation in turn leads to isolation of the internal environment and requires absolute control of the acid-base equilibrium. Any marked increase in  $P_{CO_2}$  in the internal environment gives rise to acidosis which must necessarily be compensated.

TABLE I

Temperature (° C)	OXYGEN AND CARBON DIOXIDE CAPACITANCES ( $\mu\text{M}/\text{liter}/\text{mmHg}$ )									
	Air		Distilled water		Sea water		Blood (man)		Haemolymph (crab)	
	O <sub>2</sub>	CO <sub>2</sub>	O <sub>2</sub>	CO <sub>2</sub>	O <sub>2</sub>	CO <sub>2</sub>	O <sub>2</sub>	CO <sub>2</sub>	O <sub>2</sub>	CO <sub>2</sub>
10	56.7	—	2.2	70.6	2.2	70.6	—	—	—	—
15	55.7	—	—	—	—	—	—	—	30	300
37	51.7	—	1.4	33.5	—	—	42	330	—	to 1600

water-breathing animals, however, the value of the  $P_{\text{CO}_2}$  change never exceeds a few torr, even when the  $\text{O}_2$  extraction coefficient from water is close to maximal (Fig. 1).

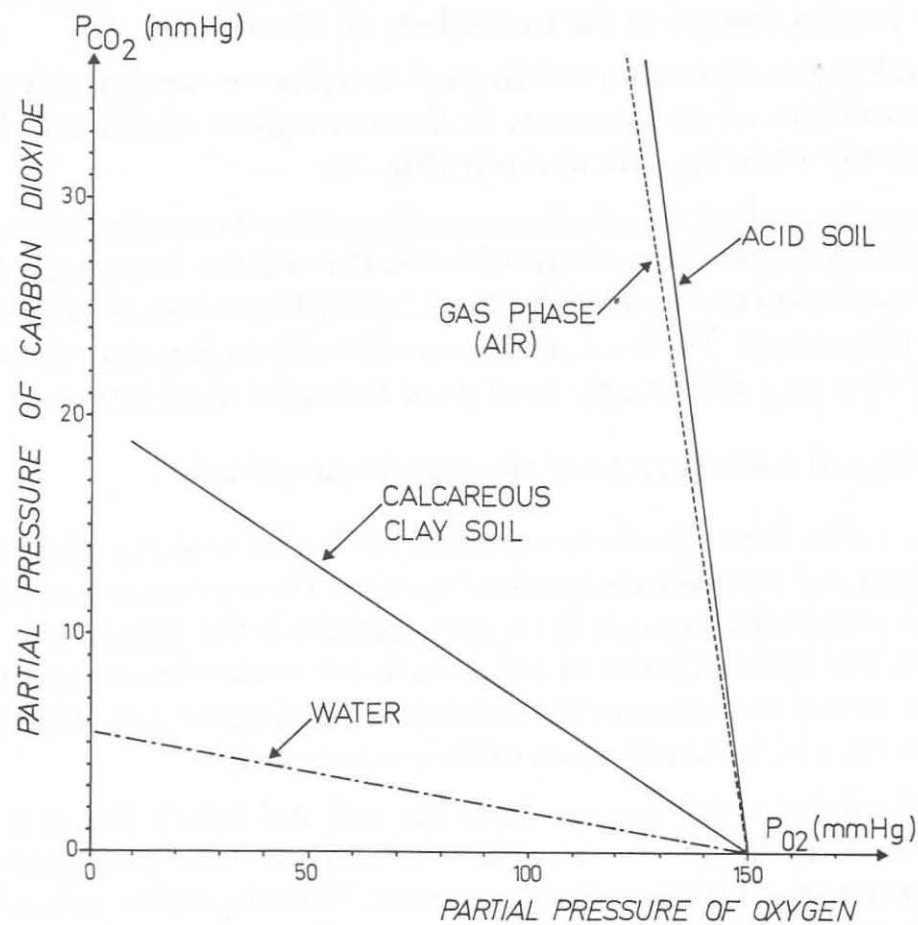


Figure 1  $P_{\text{CO}_2}$  vs  $P_{\text{O}_2}$  diagram of gas exchange by diffusion in air, in water (redrawn from DEJOURS, 1975) and in soils (redrawn from VERDIER, 1975). Acid soil behaves like a gaseous system and calcareous clay soil more like a water system.

In a well-aerated soil, whether of acidic or of calcareous clay type, diffusion processes continually renew the air in the soil. Under these conditions  $P_{O_2}$  is high, and  $P_{CO_2}$  remains low (4 to 5 mm Hg maximum in the upper layers of the soil). The atmosphere of the soil is saturated with water vapour and animal species relying on cutaneous respiration can develop without restraint, as can aquatic forms such as nematodes and aerial forms such as collembolans.

When these same soils are flooded, or where drainage is poor, animals rapidly find themselves in confined spaces and living conditions are drastically changed.

In an acid soil, the hypercapnia provoked by the elevation of  $P_{CO_2}$  can exert a selective influence on the soil fauna, favouring species possessing adaptive mechanisms (reduction in metabolic level, autoregulation of the acid-base balance). It seems likely that such species are  $CO_2$ -independent. The collembolan *Onychiurus armatus*, which is habitually found in acid soil (PONGE, personal communication) tolerates  $CO_2$  concentrations up to 35 % (RUPPEL, 1953). The weak capacitance of acid soils for  $CO_2$  must be compensated by high capacitance and an augmented buffering capacity of haemolymph.

In a poorly-aerated calcareous clay soil, the situation is very different and the dynamic changes in the soil atmosphere are comparable to those of gases exchanged with the environment,  $P_{CO_2}$  varies very little in comparison to  $P_{O_2}$ . This type of soil, just like sea-water, ensures through its capacitance a low  $P_{CO_2}$  which favours the presence of animal species that are sensitive to carbon dioxide; that is, those which have a weak capacitance in their internal environment (a characteristic of the aquatic mode of respiration). The collembolan *Onychiurus granulatus*, which is mainly found in neutral calcareous clay soils, is more sensitive to  $CO_2$  than *Onychiurus armatus*. MOURSI (1962) has demonstrated that a  $CO_2$  concentration of 1.7 % is fatal for *Onychiurus granulatus*.

As a general rule, surface-living collembolans seem to be more sensitive to  $CO_2$  than species which live deep in the soil (ZINKLER, 1966). In addition, it is found that calcareous clay soils are more frequently found to have microarthropods living deep down than are acid soils (PONGE, personal communication).

In order to achieve a better understanding of soil animals with respect to oxygen, it is necessary to consider the phylogenetic history of respiration. At the beginning of the Palaeozoic era, some 600 millions years ago, the partial pressure of  $O_2$  in water and air reached 1.5 torr, i.e. one hundredth of the modern sea-level value. This was sufficient for some cells to shift from fermentative to aerobic metabolism (DEJOURS, 1975).

The first metazoans appeared during the Cambrian when  $P_{O_2}$  exceeded 1.5 torr (the « Pasteur point ») and aquatic life diversified in the range from 1.5 to 15 torr. Aerial life emerged at the end of the Ordovician when  $P_{O_2}$  attained 14 torr, with the

appearance of the first terrestrial arthropods such as the scorpions. The first insects like the collembolan *Rhyniella praecursor* (MASSOUD, 1967) developed during the Devonian when  $P_{O_2}$  was 35 torr; that is, in an atmosphere containing 4.5 % oxygen. It was only during the Carboniferous, 300 millions years ago, that  $P_{O_2}$  reached its modern level of 160 torr. It is believed that there was little subsequent change in  $P_{CO_2}$  from that time until the present day (SCHIDLOWSKI, 1980).

Today, oxygenation conditions can be considered as hyperoxic for many primitive forms living in soils. It is therefore not surprising to find evidence that some species have the capacity to cope with certain hypoxic conditions. For instance, the oxygen consumption of collembolans begins to fall only when the oxygen concentration is less than 5 % or approximately 38 mm Hg (ZINKLER, 1966). Soil nematodes can survive under sub-anaerobic living conditions (RHODE, 1971). The survival capacity of many invertebrates placed in pure nitrogen can also be interpreted as an adaptation of primitive forms for coping with great fluctuations in  $P_{O_2}$ .

In conclusion, I would like to emphasize the fact that the notion of capacitance borrowed from physiologists and applied to edaphic environments allow us to establish new relationships between the fauna and its environment. I shall leave it to soil specialists to make what they can of the hypothesis deriving from the above analysis, namely that acid soils would seem to be the transitional medium for conquest of the aerial environment. Calcareous clay soils, on the other hand, can be considered as refuge environments which preserve the conditions of sub-aquatic life.

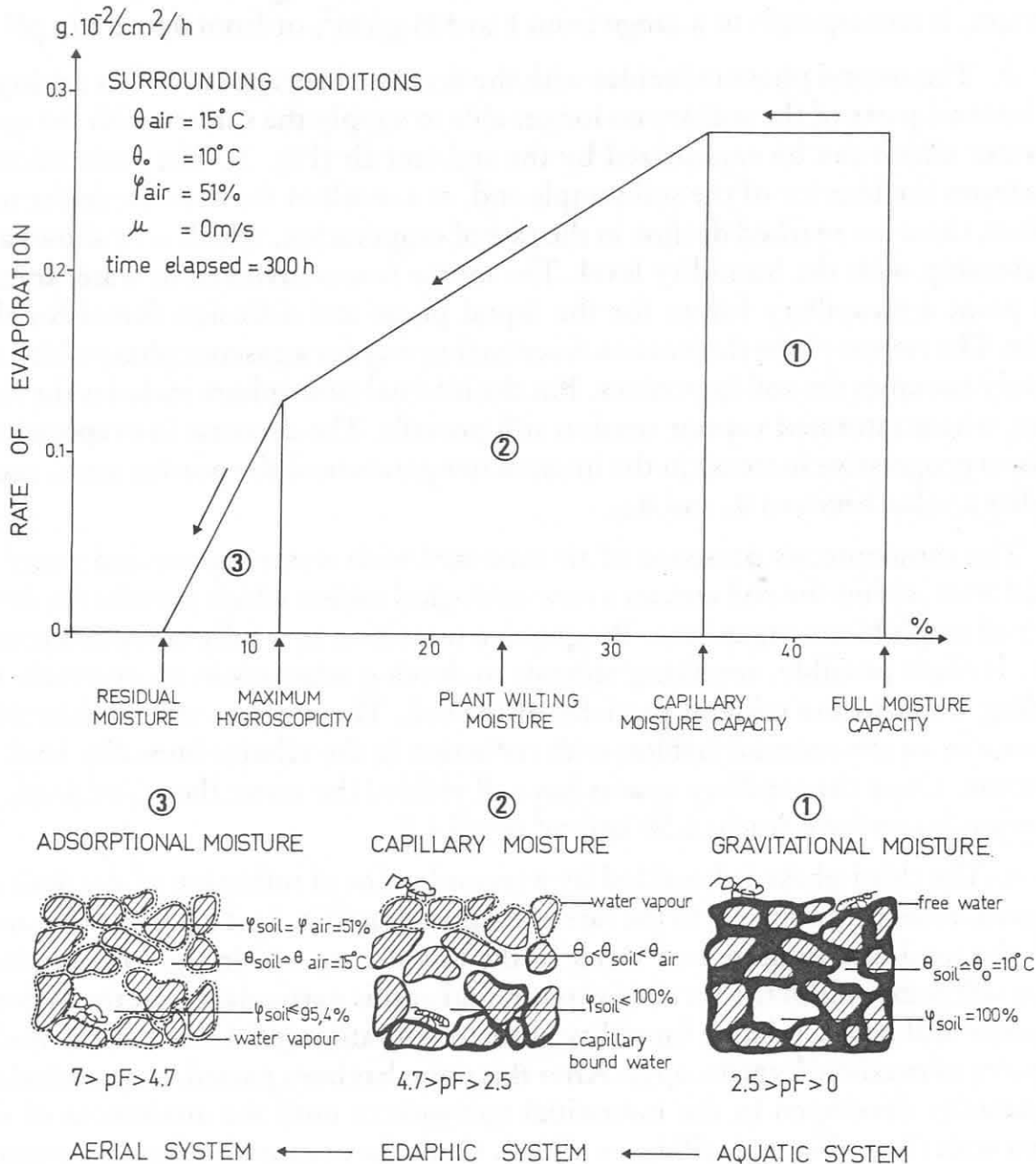
### 3. Dynamic study of the principal states of water in the soil : the notion of the porosphere

As with the study of transpiration of soil animals, the experimental approach is based on continuous weighing of a slab of soil (20 x 10 x 2.5 cm) using a recording electrobalance under isobaric and isothermic conditions. On the basis of the crude data curve produced by the apparatus, one can derive an initial diagram representing change in the water content of the soil as a function of time, but the value of this diagram is relatively limited. A more detailed picture of the desiccation process is obtained by following changes in unidirectional evaporative flux as a function of change in the water content of the soil. It emerges, in fact, that the desiccation of a slab of soil is a polyphasic phenomenon in which three categories of water succeed one another : gravitational water, then capillary water, and finally hygroscopic water (VANNIER, 1970, 1971, 1978) :

a. The first phase characterises soils which are soaked with water (Fig. 2). The evaporative flux (g) is constant, independently of the nature of the substrate. Elimination of water follows the same laws as those governing evaporation from a free water surface and the desiccation front is located at the surface of the soil sample. The liberation of water molecules is an endothermic phenomenon and the temperature of the



substrate ( $\theta_{\text{soil}}$ ) is constant, equalling the limiting cooling temperature ( $\theta_o$ ), whose value depends upon the partial pressure of water vapour in the surrounding air. In other words, it depends upon the relative humidity ( $\Phi_{\text{air}}$ ) and the ambient temperature ( $\theta_{\text{air}}$ ) of the air. The relative humidity of air in the macropores, in contact with the evaporation front (limiting layer), is 100 % or at least very close to the saturation point.



**Figure 2** Unidirectional drying of a slab of soil (20 x 10 x 2.5 cm). The three phases of the evaporation process illustrate the progressive passage from an aquatic system to an aerial system.  $\theta_{\text{air}}$  = dry temperature;  $\theta_o$  = wet temperature due to the cooling effect of evaporation; ( $\Phi$ ) = relative humidity (in air or soil),  $pF$  = logarithm of the height in centimeters of a column of water corresponding to the suction;  $u$  = air turbulence.

At the soil surface, as within open cavities, small animals therefore find themselves in an atmosphere saturated with water vapour. At this stage, the soil favours the development of aquatic and subaquatic species. Extraction of water requires energy expenditure to overcome forces of superficial friction, intermolecular attraction forces, and so on. During the first phase, this energy expenditure is relatively limited. When expressed in the form of suction measured as the height of an equivalent column of water, it corresponds to a range from 1 to 346 g/cm<sup>2</sup>, or from 0 to 2.5 in pF units.

*b.* The second phase coincides with the decrease in evaporative flux arising when the internal parts of the soil are no longer able to supply the surface with the quantity of water which can be vapourized by the ambient air (Fig. 2). The desiccation front penetrates the interior of the soil sample and, as a result of the decrease in the transfer surface, there is a marked decline in the rate of evaporation, which now shows a linear relationship with the humidity level. The motor forces involved in water transfer at this point are capillary forces for the liquid phase and diffusion forces for the gas phase. The retreat of the desiccation front makes way for a gaseous phase which subsequently occupies the soil interstices. But the internal atmosphere includes the limiting layer, where saturated vapour tension still prevails. The decrease in evaporation rate leads to progressive increase in the internal temperature of the porous mass, such that  $\theta_{\text{soil}}$  has a value between  $\theta_o$  and  $\theta_{\text{air}}$ .

The simultaneous presence of air saturated with water vapour and water in the liquid state within the soil creates a new ecological milieu which permits the development of amphibious organisms. Progressive transition to a fully aerial mode of existence is made possible, requiring animals to develop adaptations to overcome forces binding water to the mineral particles of the soil. These forces are considerable and increase in an exponential fashion with reduction in the relative humidity level of the substrate. Once the capillary spaces have all yielded the water they contained, water retention forces have reached 50 kg/cm<sup>2</sup> or pF 4.7.

*c.* The third phase is heralded by a second point of inflection of the desiccation diagram, reflecting a change in the rate of evaporation (Fig. 2). This situation coincides with the total disappearance of water in the liquid state within the soil sample. Any water still present is in the form of vapour, and at this particular point the majority of the pores still have a relative humidity close to saturation (pF 4.7 is also referred to as the point of maximal hygroscopy). After this point has been passed, a saturation deficit is gradually developed in the interstitial atmosphere until the attainment of equilibrium with the ambient air ( $\Phi_{\text{soil}} = \Phi_{\text{air}}$ ). Once the evaporative flux has ceased ( $g = 0$ ), the internal temperature will have come to match that of the surrounding air and will subsequently follow its fluctuations closely.

Whilst this hygroscopic equilibrium is being established, the soil animals are forced to combat a severe loss of body water arising from evaporation through their integuments. At the same time, they must perform a considerable amount of work in

order to extract the water molecules absorbed on the linings of the soil cavities. At pF 5, when the relative humidity of the air has fallen to 93 %, a suction force of 100 kg/cm<sup>2</sup> must be exerted to extract water; at pF 6, with a relative humidity of 43.4 %, the force required has reached 1 ton/cm<sup>2</sup>.

#### 4. Consequences of the thermodynamic properties of the soil for the evolution of animal species

The desiccation process just described is characteristic of all hygroscopic materials and of bodies with fine or medium porosity (KRISCHER, 1959). The soil is one member of the group of porous bodies which appeared at the interfaces between the lithosphere and the hydrosphere, and between the lithosphere and the atmosphere, as a result of the combined physical, chemical, and biological mechanisms of erosion. For a physicists, porous bodies are solids with an internal surface which endows them with a remarkable set of hygroscopic properties. For example, a clay such as bentonite has an internal surface in excess of 800 m<sup>2</sup>/g and a clay soil containing 72 % montmorillonite possesses an internal surface equal to 579 m<sup>2</sup>/g (FINK *et al.*, 1968). The capacity to condense gases on the free walls of capillary spaces (the phenomenon of adsorption) permits porous bodies to reconstitute water reserves from atmospheric water vapour. In my view, the porous state represents a specific state of matter occupying the same rank as the three other fundamental constituents of our planet (rock, or the lithosphere; water or the hydrosphere; and air, or the atmosphere). I have proposed the term *porosphere* as a collective category for all solids with an internal surface (VANNIER, 1973).

The succession of hydric states described above shows that porous bodies such as the soil permit slow, gradual transition from an aquatic system towards a xeric aerial system. From the ecological point of view, the first phase of evaporation corresponds to a period in which aquatic forms can develop without risk (Fig. 2). The second phase corresponds to a period of transition during which aerial and aquatic forms can coexist and which characterises the conditions of life present in an edaphic system. Finally, the third phase is a period which reproduces the conditions of aerial life in which water in the liquid state is no longer available and in which animals must defend themselves against the evaporative power of the air (Fig. 2).

Most orders of the animal kingdom contain representatives which have engaged on the contest of free aerial environments, but their undertaking was only crowned with success after long and lingering adaptation in a biotope offering conditions intermediate between those of the hydrosphere and those of the atmosphere. « Terrestrial life is a perpetual conflict between the need for oxygen and the need for water, since the very conditions which favour the entry of oxygen into the organism also favour water loss » (MALDAGUE, 1970). Many zoologists believe that transition to free

aerial conditions could only take place in a transitional environment bridging water and the atmosphere. (GHILAROV, 1958; CROGHAN, 1959; RAPOPORT & TSCHAPEK, 1967).

In setting out the principal stages of the phylogenetic history of respiration, I indicated that it was the invertebrates which first undertook and achieved the conquest of aerial conditions at the beginning of the Palaeozoic era. It is the invertebrates which still provide today the greatest number of living examples, usually living in the soil, whose mode of life is half-way between aquatic and terrestrial living conditions.

In the course of this session, Professor GHILAROV — a specialist in the evolution of terrestrial faunas — will be reviewing the main physiological adaptations which have permitted soil invertebrates to become independent of aquatic conditions and to engage in the conquest of terrestrial environments.

The great transition which took place in the biosphere from aquatic environment — to terrestrial conditions preceded the formation of the soils with which we are familiar nowadays. A large number of these soils developed when the angiosperms made their appearance during the Tertiary era. The term « porosphere » designates the products of desintegration of crystalline or sedimentary rocks, such as muds, silts, volcanic powders, aeolian dusts, sands, soils, etc... These products greatly facilitated the establishment of the first chlorophyll – bearing plants on the surfaces of the continents well before the emergence of the invertebrates, later followed by the vertebrates.

If the three primary constitutive elements of the Earth (rocks, water and the atmosphere) had exhibited abrupt contact interfaces without any zones of erosion, it is likely that faunas and floras would have evolved in directions rather different from those which we can discern around us today. Direct passage, without intermediate stages, from an aquatic environment to the atmosphere was probably achieved for the first time by the gastropods, a very ancient zoological group. But the acquisition of a shell doubtless represents the most effective solution for living in the atmosphere while making use of the thermodynamic properties of porous bodies. As a general rule, all the animal forms which now live in free air at some time or other had close links with the porosphere, either during phylogeny or during ontogeny.

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